Acta Botanica Brasilica 29(3): 375-382. 2015.
doi: 10.1590/0102-33062014abb0045

Effect of water stress on seedling growth in two species with different abundances: the importance of Stress Resistance Syndrome in seasonally dry tropical forest

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Received: December 10, 2014. Accepted: April 7, 2015

ABSTRACT

In seasonally dry tropical forests, species carrying attributes of Stress Resistance Syndrome (SRS) may have ecological advantages over species demanding high quantities of resources. In such forests, *Poincianella bracteosa* is abundant, while *Libidibia ferrea* has low abundance; therefore, we hypothesized that *P. bracteosa* has characteristics of low-resource species, while *L. ferrea* has characteristics of high-resource species. To test this hypothesis, we assessed morphological and physiological traits of seedlings of these species under different water regimes (100%, 70%, 40%, and 10% field capacity) over 85 days. For most of the studied variables we observed significant decreases with increasing water stress, and these reductions were greater in *L. ferrea*. As expected, *L. ferrea* maximized their growth with increased water supply, while *P. bracteosa* maintained slower growth and had minor adjustments in biomass allocation, characteristics representative of low-resource species that are less sensitive to stress. We observed that specific leaf area, biomass allocation to roots, and root/shoot ratio were higher in *L. ferrea*, while biomass allocation to leaves and photosynthesis were higher in *P. bracteosa.* Results suggest that the attributes of SRS can facilitate high abundance of *P. bracteosa* in dry forest.

Keywords: abundance, high-resource species, *Libidibia ferrea,* low-resource species, morphological traits, physiological traits, *Poincianella bracteosa*, Stress Resistance Syndrome, water stress

Introduction

The distribution and abundance of plant species are determined, in large part, during initial regeneration stages, when seedlings and young plants are more vulnerable to environmental conditions and incur on higher mortality rates associated with various biotic and abiotic factors (Harper 1977; Kitajima & Fenner 2000). Such factors may act as stressors, exerting deleterious effects on plant growth and development (Larcher 2006; Kranner *et al.* 2010; Taiz & Zeiger 2013).

Stress is characterized as a significant deviation from the optimal conditions for life, which induces changes and responses in all functional levels of the organism (Larcher 2006; Kranner *et al.* 2010). Drought (Figueirôa *et al.* 2004; Sausen & Rosa 2010), salinity (Ahmad *et al.* 2010), extreme temperatures (Keles & Öncel 2002), oxygen deficiency (Mustroph & Albrecht 2003), and heavy metals excess in soil (Roychoudhury *et al.* 2012) are some of the major abiotic or environmental sources of stress that restrict plant metabolism and growth. When these factors exceed optimum tolerance levels, the effects of stress can be manifested in plant development, structure, physiological, and biochemical processes.

Among abiotic factors, drought is considered the main obstacle to plant establishment (Moles & Westoby 2004), especially in seasonally dry tropical forests (SDTFs). The SDTF of northeastern Brazil (caatinga) occurs under a prevailing semiarid climate with high evapotranspiration potential (1500–2000 mm year^{-1}) and low precipitation (300–1000 mm year^{-1}) that is usually concentrated within 3–5 months (Sampaio 1995). Rainfall patterns during the wet season are also characterized by heavy rainfall events (exceeding 100 mm) in a single day and irregular seasonality (i.e., the rainy season may start and end at different months between years) (Sampaio 2010). Thus, the inconstancy of

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the first rains and the occurrence of dry spells during the rainy season are significant causes of mortality of seeds and seedlings by desiccation (McLaren & McDonald 2003; Vieira & Scariot 2006).

The effects of drought are highly variable depending on length, speed of stress imposition, and stage of plant development, and plants respond to stress through a complex net of physiological and morphological changes (Pimentel 2004). During evolution, many tree species have developed various mechanisms to enhance drought adaptation, including well-developed root systems, growth rate adjustment, plant structure modifications, and increased water use efficiency (Yin *et al.* 2005).

According to the stress resistance syndrome (SRS), species adapted to low-resource environments (water, nutrient, or light limitations) present a set of attributes, such as low rates of photosynthesis, low nutrient uptake, low tissue turnover, high leaf longevity, high root/shoot ratio, high ability to accumulate reserves, production of small and thick leaves, and high investments in secondary defense compounds (Chapin III 1980; Coley *et al.* 1985; Chapin III *et al.* 1993; Aerts & Chapin III 2000). Species adapted to low-resource environments tend to respond little relatively to variations in resource availability, showing low phenotypic plasticity (Chapin III *et al.* 1993). These species grow slowly even when they have ideal resource supplies because they divert resources to other functions besides growth, especially storage or defense. Thus, such species tend to conserve resources under unfavorable conditions, which increase survival at the expense of vegetative growth (Chapin III 1980; Lambers & Poorter 1992; Aerts & Peijl 1993; Chapin III et al. 1993; Valladares *et al.* 2000; Pearson *et al.* 2003). In contrast, plants adapted to high-resource environments have characteristics such as high rates of photosynthesis, high nutrient uptake, high tissue turnover, low leaf longevity, and low root/shoot ratio. These species are typically more plastic, modifying allocation patterns to increase resource acquisition (Chapin III 1980; Chapin III *et al.* 1993).

Species that occur in SDTFs and possess SRS attributes may have ecological advantages (growth and survival) under water stress conditions, allowing them to maintain higher abundances than species that do not possess these attributes (high resource-species). Phytosociological studies in caatinga show that *Poincianella bracteosa* is a species with a high abundance of individuals where water resources are limited (Mendes 2003; Moreira *et al.* 2007; Lima 2011; Costa & Araújo 2012), while *Libidibia ferrea* has low abundances in these areas and preferentially occurs on the banks of temporary rivers (Queiroz 2009). Such abundance differences between species may be related to different strategies to cope with drought. Thus, we hypothesized that *P. bracteosa* has characteristics of a low-resource species, allowing it to be less affected by water stress than *L. ferrea*, which we characterized as a high-resource species. To test this hypothesis, we assessed morphological and physiological traits during the initial growth of seedling of these species in different water regimes. If resource use strategies are indeed related to stress tolerance, we expect to find low-resource species showing little variation in morphological and physiological traits, while high-resource species should respond positively to increased water availability.

Material and methods

Site and studied species

The experiment was conducted from September to December 2013 in a greenhouse located at the Meteorological Station of the Federal University of Ceara, in the city of Fortaleza (3°43′02′′S - 38°32′35′′W).

Both the studied species belong to the family Fabaceae, subfamily Caesalpinioideae. *Poincianella bracteosa* (Tul.) L.P. Queiroz is a deciduous tree found mainly in dry formations such as caatinga, cerrado, seasonal forests, and coastal dunes (Queiroz 2009). *Libidibia ferrea* (Mart. ex Tul.) L.P. Queiroz is a semi-deciduous tree that prefers loamy soils and is found primarily in the margins of temporary rivers and less frequently in caatinga (Maia 2004; Queiroz 2009).

The fruits of the species were collected from July to September 2013 in mature individuals, located in an area of caatinga at Fazenda Experimental Vale do Curu, Pentecoste, Brazil (3°47′34′′S - 39°16′13′′W). The seeds were removed and stored in a chamber with controlled temperature (10°C and 60% relative humidity) until the beginning of the experiment. Fertile branches were collected for accurate species identification. *L. ferrea* and *P. bracteosa* were incorporated into the collections of the Herbarium Prisco Bezerra of Federal University of Ceara with vouchers 54707 and 54708, respectively.

Experimental design

The experimental design was a randomized block with four replicates, arranged in subplots. The plots were formed by the two species (*P. bracteosa* and *L. ferrea*) and the subplots by four irrigation regimes (100%, 70%, 40%, and 10% field capacity). Each subplot was represented by three pots with one plant per pot. Therefore, 96 plants were used in total (4 blocks x 2 species x 4 treatments x 3 plants per treatment).

On September 21, seeds of *L. ferrea* and *P. bracteosa* were sown in trays (128 cells) containing a mixture of sand and compost (2:1). *L. ferrea* seeds were scarified with sandpaper to overcome physical dormancy. Ten days after sowing (01-October), emerging seedlings had two fully expanded leaves and were transplanted into pots with 7 L capacity (32.5 cm high × 16 cm wide on top × 11 cm wide in the base), and filled with 8 kg of dry soil, collected from the same caatinga area where the seeds were collected.

The soil was collected at 30 cm depth, and showed a sandy loam texture and the following properties: pH = 6.1, P = 5 mg kg^{-1}, and Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} of 3.2, 1.2, 0.17, and 0.42 cmol$_c$ kg^{-1}, respectively.

After transplanting, all pots were irrigated at field capacity (FC) during five days for acclimatization, and then subjected to four irrigation levels: 100%, 70%, 40%, and 10% FC, hereafter referred to as T_{100}, T_{70}, T_{40}, and T_{10}, respectively. The field capacity of soil was previously determined using the direct gravimetric method (Souza *et al.* 2000). The maximum water retention capacity in 8 kg of soil was 1.3 L; thus, the T_{100} treatment pots had a weight of 9.3 kg. The other treatments showed the following amounts of water and weight: T_{70}= 0.91 L; 8.91 kg, T_{40}= 0.52 L; 8.52 kg, and T_{10}= 0.13 L; 8.13 kg.

Water levels were monitored every 48 h, by weighing the pots on a balance with 5 g accuracy and the amount of water evapotranspired was reset based on the difference between the actual weight of the pot and the prefixed weight for each treatment, assuming the water had a weight:volume ratio of 1:1. Throughout the experimental period, the temperature data and relative humidity (RH) were recorded every 10 minutes by a data-logger (HOBO®, Onset) installed inside the greenhouse. Mean minimum and maximum temperatures measured were 25 and 36°C, and the mean minimum and maximum RH were 41% and 82%, respectively.

Morphological measurements

Measurements of ecophysiological traits were taken at 85 days after treatment initiation, corresponding to 100 days after sowing. The seedling height was measured between the soil surface and insertion of the last leaf, and the stem diameter was measured at ground level. All fully expanded leaves were counted.

The total leaf area (*LA*) was assessed using a leaf area meter (LI-COR®, model LI-3100C). Roots were washed and the clods of soil attached to the roots were broken carefully to avoid root loss. All plant material was placed separately in an oven at 80°C for 48 h and then weighed on a precision balance to 0.01g.

The total dry mass (*TDM*) was calculated as the sum of the dry mass of leaves (DM_L), stems (DM_S), and roots (DM_R). The biomass allocation in each part of the plant was calculated as the percentage of leaves (BA_L), stems (BA_S), and roots (BA_R) in relation to *TDM*. The root/shoot ratio was $(R/S) = DM_R/(DM_L + DM_S)$ and the specific leaf area $(SLA) = LA/DM_L$ (Cornelissen *et al.* 2003).

The relative growth rate (*RGR*) was calculated as: $(\ln M_2 - \ln M_1)/(t_2 - t_1)$, where M_1 and M_2 represent final and initial mass total; t_1 and t_2 to the end and start time. For each species, "proportional growth" was calculated as the ratio of the average *TDM* obtained in each treatment with water restriction (T_{10}, T_{40}, T_{70}) over the control (T_{100}). This calculation was based on Munns (2002) who reported that stress tolerance could be assessed as the proportion of biomass production under stress conditions compared to that produced under control conditions.

Physiological measurements

Measurements of stomatal conductance (*gs*), transpiration (*E*), and photosynthesis (*A*) were carried out using an infrared gas analyzer (IRGA ADC system, Hoddesdon, UK) coupled to a source of artificial light with an intensity of approximately 1300 µmol m^{-2} s^{-1}. The evaluations were performed between 09:00 and 12:00 am, in the third fully expanded leaf pair from the apex to base, and water-use efficiency (*WUE*) was obtained by the A/E ratio (Larcher 2006).

Data analysis

Data were analyzed using a two-way ANOVA (species and water status were considered as factors), addressing the effects of the interaction, as well as differences between species and for each species between water status treatments. The means were compared by Tukey test at 5% probability (Banzatto & Kronka 2006), using the Assistat software (beta version 7.7). Data that did not meet the assumption of normality were transformed to ln (x + 1), but the original data is presented in all graphs.

Results

Morphological measurements

The interaction between species and irrigation levels was statistically significant in the following morphological measurements: height, diameter, number of leaves, *LA*, *TDM*, *RGR*, and BA_S (Tab. 1).

In both species, the height of the seedlings increased significantly with water supply (Fig. 1A). In relation to T_{10}, the height of *P. bracteosa* seedlings significantly increased in all treatments by 52, 72, and 80% in T_{40}, T_{70}, and T_{100}, respectively. In *L. ferrea*, the height increased by 76, 86, and 87% in T_{40}, T_{70}, and T_{100}, but T_{100} and T_{70} did not differ from each other. The fact that the percentages were higher in *L. ferrea* shows that this species is capable of maximizing growth with increased resources, while *P. bracteosa* maintained slower growth rates.

Stem diameter also increased proportionally to the supply of water for both species (Fig. 1B). In relation to T_{10}, the diameter of *P. bracteosa* seedlings significantly increased in each treatment by 51, 62, and 73% in T_{40}, T_{70}, and T_{100}, respectively. In *L. ferrea*, the stem diameter increased by 56, 72 and 74% in T_{40}, T_{70} and T_{100}, respectively, and similar to the results in height, there were no significant differences between T_{70} and T_{100}. Interspecific differences only occurred in T_{40} and T_{70}, with *P. bracteosa* maintaining the lowest averages.

Table 1. Mean square of growth and gas exchange variables in seedlings of *L. ferrea* and *P. bracteosa* subjected to four irrigation regimes (10%, 40%, 70%, and 100% of field capacity) for 85 days.
* Significant at 5%, ** Significant at 1%, NS not significant. Degree of freedom (df), leaf area (*LA*), specific leaf area (*SLA*), total dry matter (*TDM*), relative growth rate (*RGR*), biomass allocation to leaves (BA_L), stem (BA_S) and roots (BA_R), root/shoot ratio (*R/S*), stomatal conductance (*gs*), transpiration (*E*), photosynthesis (*A*), and water-use efficiency (*WUE*).

Variables	Sources of variation					
	Block	Species (A)	Residual-a	Irrigation levels (B)	Interaction (A)x(B)	Residual-b
Height	0.00191^{NS}	5.59637**	0.00195	4.79896**	0.20373**	0.01231
Diameter	0.00120^{NS}	0.02099*	0.00159	1.64418**	0.00691*	0.00192
Nº leaves	0.00195^{NS}	2.49247**	0.00243	1.76481**	0.04828*	0.01475
LA	0.00635^{NS}	0.88038**	0.01926	13.02854**	0.05035*	0.01531
SLA	103.953^{NS}	25646.89**	225.354	1540.8912**	294.6748^{NS}	136.3905
TDM	0.00351^{NS}	1.08693**	0.00460	10.74152**	0.09041**	0.00814
RGR	0.00001^{NS}	0.00007^{NS}	0.00003	0.00284**	0.00007**	0.00001
BA_L	6.52419^{NS}	1605.92537**	6.97773	36.74079*	23.03355^{NS}	9.40258
BA_S	4.33577*	373.93290**	0.37134	183.65043**	73.25856**	5.41020
BA_R	18.76650^{NS}	430.00846**	8.60188	60.19875^{NS}	15.42913^{NS}	18.83149
R/S ratio	0.03477^{NS}	0.63092*	0.02628	0.10613^{NS}	0.03886^{NS}	0.03018
gs	0.00283^{NS}	0.00001^{NS}	0.00617	0.14429**	0.00066^{NS}	0.00218
E	0.96494^{NS}	0.25294^{NS}	0.35666	42.42474**	0.22579^{NS}	0.32792
A	5.23057^{NS}	13.76157*	0.63175	299.28667**	4.55035^{NS}	2.55521
WUE	0.35494^{NS}	0.36583^{NS}	0.11309	0.23896*	0.01514^{NS}	0.05181
df	3	1	3	3	3	18

In relation to T_{10}, the number of leaves of *P. bracteosa* seedlings increased by 50, 60, and 69% in T_{40}, T_{70}, and T_{100} respectively, but there was no significant difference between T_{40} and T_{70}, as well as between T_{70} and T_{100} (Fig. 1C). *L. ferrea* increased the number of leaves by 67, 71, and 73% in T_{40}, T_{70} and T_{100} respectively, and these three treatments were not significantly different from each other, but they did differ from T_{10} (Fig. 1C). Comparing the two species, we observed that in all treatments the number of leaves was significantly lower in *P. bracteosa*. The T_{10} treatment also induced senescence and abscission of leaflets in *L. ferrea*, from day 55 until the end of the experiment. This phenomenon was not recorded in *P. bracteosa*, which continued producing leaflets until the end of the experiment.

The *LA* followed a similar pattern observed in the number of leaves, which increased because of the increased supply of water (Fig. 1D). In relation to T_{10}, the *LA* of *P. bracteosa* seedlings increased by 81, 92, and 94% in T_{40}, T_{70}, and $T_{100,}$ respectively, with significant differences among all treatments. In *L. ferrea*, *LA* increased by 85, 93, and 94% in T_{40}, T_{70}, and T_{100}, respectively, but there were no significant differences between T_{70} and T_{100}. Interspecific differences occurred in the T_{10}, T_{40}, and T_{70} treatments, in which *P. bracteosa* maintained the lowest values in relation *L. ferrea*.

In the *SLA*, there was no significant interaction among species and irrigation levels (Tab. 1). However, there were species differences, with *P. bracteosa* having lower overall average *SLA* than *L. ferrea* (Tab. 2).

The *TDM* increased with increased water availability, and significant differences among all treatments were observed for both species (Fig. 1E). In relation to T_{10}, *TDM* increased by 82, 94, and 96% for *P. bracteosa* seedlings and 88, 95, and 96% for *L. ferrea* seedlings in T_{40}, T_{70}, and T_{100} respectively. Interspecific differences were also found in all treatments except T_{10}, with *P. bracteosa* maintaining the lowest averages.

In both species, *RGR* showed significant differences between all treatments, except between T_{70} and T_{100} (Fig. 1F). In relation to T_{10}, the *RGR* increased by 63, 77, and 76% for *P. bracteosa* seedlings and 79, 82, and 84% for *L. ferrea* seedlings in T_{40}, T_{70}, and T_{100} respectively. Interspecific differences were only found in the T_{40} treatment, in which *P. bracteosa* obtained a lower average than *L. ferrea*.

The values of the “proportional growth” of *TDM* obtained in each treatment of water restriction in relation to T_{100} were: $T_{10}/T_{100} = 0.039$, $T_{40}/T_{100} = 0.34$, and $T_{70}/T_{100} = 0.80$ for *L. ferrea* and $T_{10}/T_{100} = 0.044$, $T_{40}/T_{100} = 0.24$, and $T_{70}/T_{100} = 0.70$ for *P. bracteosa*.

Considering all the treatments, the biomass allocation of *L. ferrea* seedlings ranged from 22–30% in leaves, 15–31% in stems, and 47–55% in roots, while *P. bracteosa* seedlings had less variation: 38–40% in leaves, 15–21% in stems, and 42–45% in roots. Thus, biomass allocation patterns showed that *P. bracteosa* seedlings are less responsive to changes in water availability, whereas *L. ferrea* seedlings make more observable adjustments (Fig. 2).

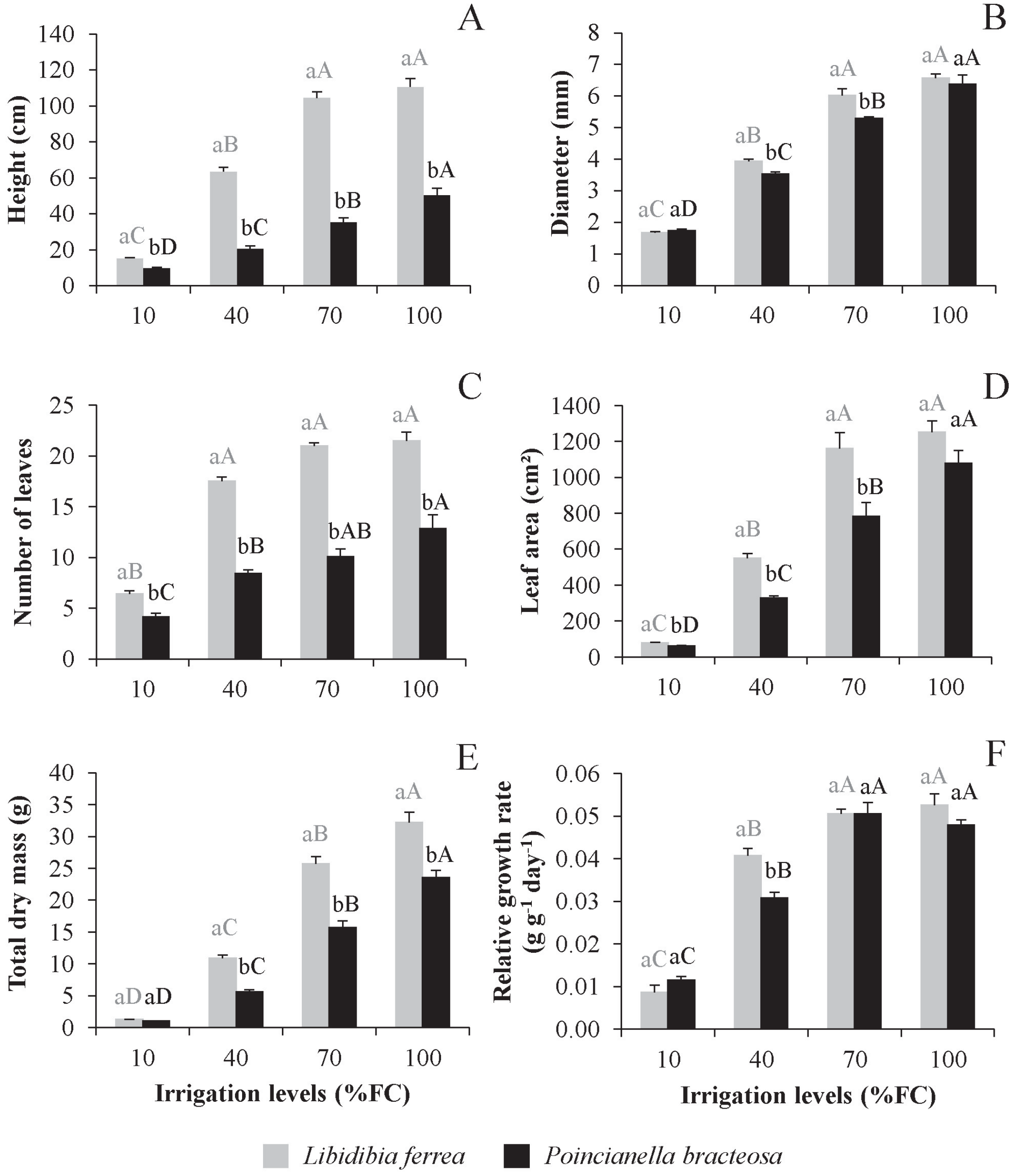

Figure 1. Height (A), diameter (B), number of leaves (C), leaf area (D), total dry mass (E), and relative growth rate (F) of seedlings of *L. ferrea* and *P. bracteosa* that, at 15 days after sowing, were subjected to four irrigation regimes (10%, 40%, 70%, and 100% of field capacity) for 85 days. Lowercase letters (compare species in the same treatment) and uppercase (compare treatments in the same species) equal, do not differ by Tukey test at 5% probability. Vertical bars indicate standard error of the mean.

The *R/S* ratio showed significant differences only between species, in which *L. ferrea* was higher than *P. bracteosa*. Thus, *L. ferrea* showed higher plasticity in the *R/S* ratio, which varied 3-fold more (T_{10}: 1.2 to T_{100}: 0.91) than *P. bracteosa* seedlings (T_{10}: 0.84 to T_{100}: 0.73).

Physiological measurements

In all variables of gas exchange (*gs*, *E*, *A*, and *WUE*), there was also no significant interaction between species and irrigation levels (Tab 1). The variables *gs*, *E*, and *A* were strongly limited by water restriction, with significant differences between all treatments, except between T_{70} and T_{100}. There were interspecific differences only for photosynthesis, in which *P. bracteosa* showed a higher photosynthetic capacity in relation to *L. ferrea* (Tab. 2).

Although the species did not differ significantly in the *WUE*, we observed that *P. bracteosa* has a tendency to be more efficient than *L. ferrea*. As for the differences between treatments, T_{40} had the highest average, but did not differ from T_{10} and T_{70}. The lowest average was in T_{100}, which also was not different from T_{10} and T_{70} (Tab. 2).

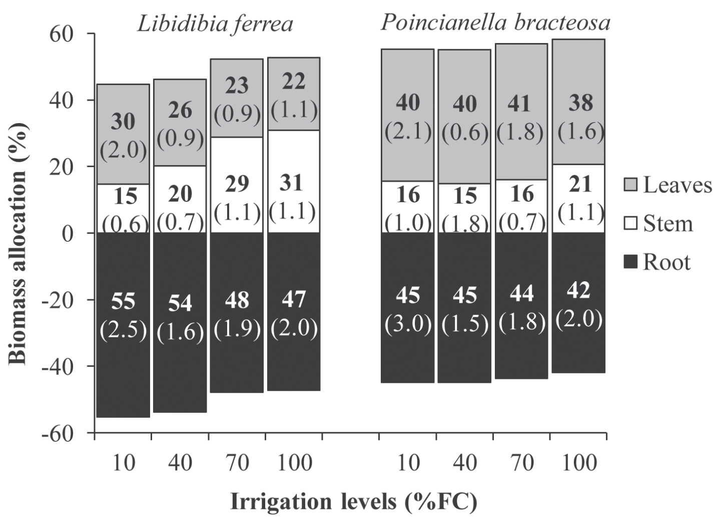

Figure 2. Biomass allocation to roots, stems, and leaves of seedlings of *L. ferrea* and *P. bracteosa* that, at 15 days after sowing, were subjected to four irrigation regimes (10%, 40%, 70%, and 100% of field capacity) for 85 days. Numbers within parentheses indicate standard error of the mean.

Table 2. Average values of growth and gas exchange traits in seedlings of *L. ferrea* and *P. bracteosa* subjected to four irrigation regimes (10%, 40%, 70%, and 100% of field capacity) for 85 days. There were no significant interactions between species and irrigation levels for any of the variables measured.
Averages with equal lowercase (species) and uppercase (treatments) letters, do not differ by Tukey test at 5% probability. Specific leaf area (*SLA*), biomass allocation to leaves (BA_L) and roots (BA_R), root/shoot ratio (*R/S*), stomatal conductance (*gs*), transpiration (*E*), photosynthesis (*A*), and water-use efficiency (*WUE*).

	SLA (cm^2/g)	BA_L	BA_R	*R/S* ratio	*gs* (mol m^{-2}s^{-1})	*E* (mmol m^{-2}s^{-1})	*A* (mmol m^{-2}s^{-1})	*WUE*
Species								
L. ferrea	194.071 a	25.342 b	50.988 a	1.076 a	0.184 a	3.578 a	9.277 b	2.624 a
P. bracteosa	137.451 b	39.511 a	43.656 b	0.795 b	0.183 a	3.756 a	10.588 a	2.838 a
Irrigation levels								
T10	180.787 A	34.789 A	50.019 A	1.059 A	0.009 C	0.447 C	1.133 C	2.683 AB
T40	173.468 AB	33.175 AB	49.299 A	1.006A	0.148 B	3.593 B	10.423 B	2.921 A
T70	158.534 BC	32.058 AB	45.460 A	0.855 A	0.268 A	5.081 A	14.218 A	2.804 AB
T100	150.255 C	29.689 B	44.508 A	0.822 A	0.308 A	5.548 A	13.956 A	2.517 B

Discussion

In general, the stress imposed by water supply limitation affected the morphological and physiological traits of both species, as it was found significant reductions in height, diameter, number of leaves, leaf area, total dry mass, and restrictions in gas exchange. Several studies with other arid and semiarid species reported similar effects caused by water stress (Silva *et al.* 2003; Cabral *et al.* 2004; Figueirôa *et al.* 2004; Gindaba *et al.* 2004; Yin *et al.* 2005; Lenhard *et al.* 2010).

Although it was not demonstrated in all studied variables, we confirmed that even with increased water supply, *P. bracteosa* presented a slower growth strategy, resembling a low-resource species, while *L. ferrea* maximized their growth, in accordance with high-resource species. According to Chapin III *et al.* (1993), compared with slow-growing species, fast-growing species have a higher dependence on new environmental resources, which make them more vulnerable to fluctuations in resource availability. Other studies have demonstrated that species of high-resource environments take advantage of the water supply increase, while species adapted to stress are less plastic (Vilela *et al.* 2003; Otieno *et al.* 2005; Villagra & Cavagnaro 2006).

Severe stress caused greater reductions in height, number of leaves, and *RGR* of *L. ferrea*, suggesting that this species is more vulnerable to water stress than *P. bracteosa*. In a study conducted in the arid zone of Argentina, water stress also caused greater reductions in growth in a species typically found in an environment with high water resources (*Prosopis alpataco*) in comparison with one from a low water resource environment (*Prosopis argentina*). In general, the studied traits were reduced by 80% in the high-resource species and 60% in the low-resource species (Villagra & Cavagnaro 2006). In another study in the savannas of Kenya, stress decreased the *TDM* and *LA* by 45 and 26% respectively in a mesic habitat species (*Acacia xanthophloea*), and by only 40 and 15% in a species that resides in xeric habitats (*Acacia tortilis*) (Otieno *et al.* 2005).

The abscission of leaflets by *L. ferrea* after 55 days in the T_{10} treatment also suggests a greater sensitivity to stress, since the early leaf fall in water deficit conditions indicates serious dehydration effects (Sala & Tenhunen 1994; Fotelli *et al.* 2000; Villagra & Cavagnaro 2006). The greater capacity of *P. bracteosa* seedlings to delay leaf abscission in T_{10} can be an advantage in relation to *L. ferrea* because after hydration *P. bracteosa* seedlings would not need to allocate assimilates to recover leaf area and may invest these resources in storage or defense functions.

The lowest *LA* and *SLA* of *P. bracteosa* seedlings reflect greater adaptation to xeric conditions than *L. ferrea* seedlings. Taiz and Zeiger (2013) report that the reduction in leaf area is an adaptive mechanism that prevents water loss and maintains hydration, since less leaf area leads to less evapotranspiration, allowing the use of limited water supply in the soil for a longer period. According Cornelissen *et al.* (2003) species from environments with low resource availability tend to have lower *SLA* than those from resource rich environments. Lower values of *SLA* tend to correspond with relatively high investments in defense of the leaf (particularly structural) and high leaf longevity (Cornelissen *et al.* 2003). There is a close association between the potential growth rate of a species and its *SLA*; therefore, *SLA* can be considered the prime factor determining interspecific variation in *RGR* (Lambers & Poorter 1992).

The *P. bracteosa* seedlings were less responsive to changes in water availability, showing minor adjustments in biomass allocation than *L. ferrea* seedlings. This is corroborated by the "proportional growth" results, in which *P. bracteosa* was higher than *L. ferrea* in T_{10} and less in T_{40} and T_{70}. Stress tolerant plants have a set of morpho-physiological traits that allow them to survive in conditions of stress, but reduce the potential for growth in the absence of it (Chapin III *et al.* 1993; Grime 1977). Thus, these species with adaptive mechanisms to stress conditions generally show less phenotypic plasticity than species not adapted. *P. bracteosa* must then have mechanisms that allow it to survive under stressful conditions, but prevent it from taking advantage in increased water availability conditions.

Studies show that plants subjected to severe water deficit invest more in root elongation than in the shoot, which increases the potential to absorb water from the deeper layers of the soil profile (Barros & Barbosa 1995; Barbosa *et al*. 2000; Silva & Nogueira 2003; Figueirôa *et al*. 2004; Villagra & Cavagnaro 2006). Contrary to what we expected, *P. bracteosa* seedlings did not present higher R/S ratio than *L. ferrea* seedlings under water stress conditions. However, the greater variation of *L. ferrea* (3-fold more than *P. bracteosa*) is in accordance with the generalization of Chapin III *et al.* (1993) that species in favorable habitats show greater plasticity in allocation patterns than species in stressful environments.

As water stress increases, plants promotes partial stomatal closure to prevent water loss by transpiration. This process alters gas exchange, limiting the availability of CO_2 within the mesophyll, thus reduces the rate of photosynthesis (Filella *et al.* 1998; Gindaba *et al.* 2004; Scalon *et al.* 2011; Taiz & Zeiger 2013). Contrary to what we expected, *P. bracteosa* seedlings had higher overall average photosynthetic rates than *L. ferrea* seedlings. This result is in accordance with other studies that demonstrated that stress-tolerant species maintained high CO_2 uptake while grown under non-limiting water availability (DeLucia & Heckathorn 1989; Patterson *et al*. 1997; Vilela *et al*. 2003), ruling out the likelihood that a *trade-off* between drought tolerance and CO_2 uptake constrains tolerant species from occupying high-resource environments. Studies indicated that the main trait associated with inherently slow-growing species from low-resource environments is low *SLA* (Lambers & Poorter 1992; Maranon & Grubb 1993; Lambers *et al*. 1998).

In general, *P. bracteosa* demonstrated attributes of a low-resource species, showing a slow growth strategy and minor adjustments in biomass allocation, and tending to have higher water use efficiency than *L. ferrea.* The attributes of the SRS can determine the success of the establishment, growth, and survival of *P. bracteosa* seedlings under water stress, favoring its high population density in the caatinga. On the other hand, the characteristics of high-resource species, such as rapid growth and high resource acquisition, make *L. ferrea* more dependent on water resources and, consequently, suffer more negative impacts when these resources become scarce. Thus, these factors may explain the low population density of *L. ferrea* in areas of caatinga, suggesting that its occurrence in this environment might be relegated to microsites with higher and more constant water availability.

Acknowledgments

We thank the Taxonomists of Herbarium Prisco Bezerra for botanical identification of species; to Raimundo Nonato Costa Ferreira for help in the planning, installation and data collection for the experiment; and to CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for providing the scholarship.

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